DISTRIBUTIONAL CHANGES AND INTERACTION BETWEEN PRAIRIE CHICKENS AND SHARP-TAILED GROUSE IN THE MIDWEST

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The "prairie grouse" of North America present an interesting example of the effects of human activities on breeding distribution patterns of birds, with resulting changes in geographic distribution and spacial isolation. Thus, the Heath Hen (*Tympanuchus cupido cupido*) was one of the most familiar birds to the early colonists, who relied heavily on it for food. Ultimately, loss of habitat caused the Heath Hen's extinction. When the vast tall-grass prairies west of the Appalachians were settled, Greater Prairie Chickens (*T. c. pinnatus*) were probably more plentiful, and greatly increased as woods were cleared and grain crops supplemented native grasses. With the further advance of settlers to the more northerly and westerly portions of the prairies, the Sharp-tailed Grouse (*Pedioecetes phasianellus*) was encountered. Unlike the Prairie Chicken, which "followed the plow," the Sharp-tailed Grouse quickly retreated before it, and thus the Prairie Chicken soon spread over a wide range that previously had been occupied by Sharp-tailed Grouse. In some areas both species found adequate habitat for survival, and their similar niche requirements resulted in increased contact between the species. The new area of contact was probably most extensive in Nebraska, the Dakotas, and the Lake States, and later spread to the Prairie Provinces of Canada. The resulting interactions between the two species in the form of ecological overlap and degree of hybridization have yet to be fully documented, but a short review of the available information would appear to be warranted. Emphasis will be placed on the situation in Nebraska, which is probably fairly representative of the Midwest as a whole.

ORIGINAL AND ACQUIRED DISTRIBUTIONS

Although it is impossible to plot original presettlement distribution patterns of the prairie grouse with complete certainty, an attempt has been made to do this for the states south of Canada (Figs. 1 and 2). Similar range maps have previously been published for these two species (Aldrich and Duvall, 1955; Aldrich, 1963), but in the case of Prairie Chickens their original ranges were not distinguished from their acquired ranges. Such a distinction was made by Baker (1953) and McClanahan (1940), and although the maps presented here were nearly completed before these were consulted, a con-

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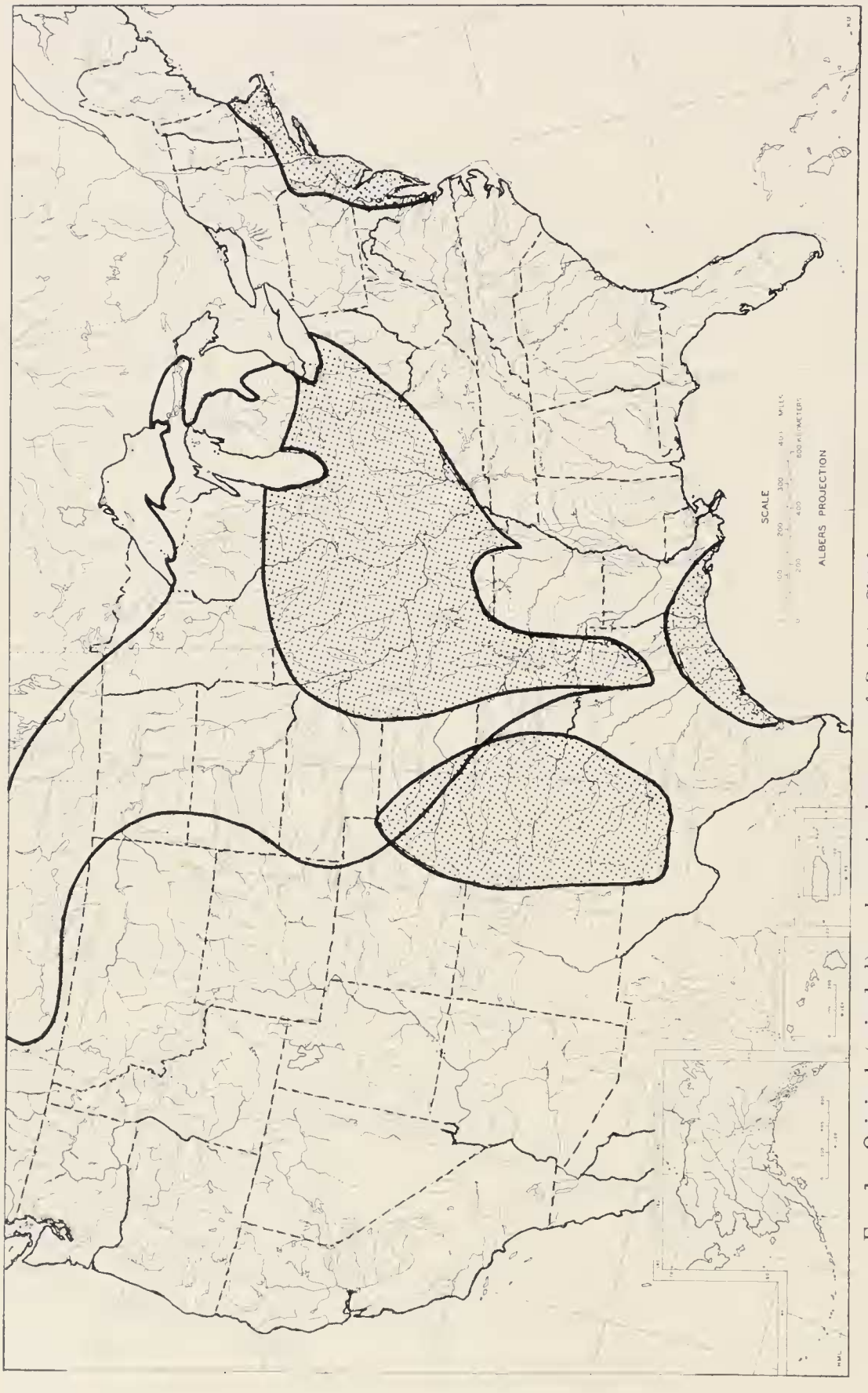

FIG. 1. Original (stippled) and acquired ranges of Prairie Chickens in southern North America.

FIG. 2. Original (shaded) and acquired ranges of Sharp-tailed Grouse in southern North America. The indicated break in range between the Plains and Columbian races of Sharp-tailed Grouse is conjectural.

siderable degree of agreement with them exists. Following the precedent of Aldrich, the Lesser Prairie Chicken (*T. pallidicinctus*) is included as if it were a geographic race of *T. cupido*, although there is still considerable doubt as to its actual systematic status. The Gulf Coast population of Attwater's Prairie Chicken (*T. c. attwateri*) is now universally regarded as a race of *T. cupido*. The southern and eastern boundary of the breeding range of the Greater Prairie Chicken is of less immediate significance than its northern and western boundaries. Baker's (1953) map agrees closely with ours in regard to the original western boundary, but extends a shorter distance north in Iowa, Wisconsin, and Michigan. Since these states, plus Illinois and possibly Minnesota, present the only areas of original possible sympatry between Prairie Chickens and Sharptails, the question is of special significance. Evidently Lewis and Clark observed Prairie Chickens as far north as the James River near Yankton, South Dakota (Burroughs, 1961) and, additionally, Coues (1874) reported that between Fort Randall and Yankton a dividing line between the two species' ranges could be drawn. Prairie Chickens evidently originally bred in northern Iowa almost to the Minnesota border, but Roberts (1932) believed that the species did not enter southeastern Minnesota until sometime prior to the middle of the nineteenth century. However, Leopold (1931) suggested that the region around St. Paul may have been the original northern limits of Prairie Chicken range, and he plotted a line suggesting that the original boundary between the two species extended from that area southeastward along Wisconsin's western tier of counties and across the northern tier of Illinois' counties toward Chicago. There is no doubt that Prairie Chickens occurred at least as far north as central Illinois in the 1830's, and that Sharp-tailed Grouse extended in wooded areas south to Chicago, indicating a definite zone of original sympatry in northern Illinois. Leopold suggested that within this zone of overlap a significant ecological separation occurred, with Sharptails occupying the "oak openings" and the Prairie Chickens found in typical prairie habitats. Schorger (1944) hypothesized a more northerly original Wisconsin range of Prairie Chickens, extending roughly across the middle of the state. In Michigan the Prairie Chicken probably originally occurred only in scattered grassy openings in the two southernmost tiers of counties (Ammann, 1957).

The probable early southern breeding limit of Sharp-tailed Grouse is obscured by their migratory movements but evidently included much of Kansas and Nebraska, nearly all of South Dakota (Coues, 1874), perhaps northern Iowa (McClanahan, 1940), essentially all of Minnesota (Roberts, 1932), and most or all of Wisconsin (Schorger, 1944). However, upper Michigan was probably later colonized by Sharptails in the early 1900's

(Ammann, 1957), as fires and logging activities cleared the forests. This last region apparently represents the only area in the United States where the Sharp-tailed Grouse has acquired any important new breeding range.

In contrast to the Sharp-tailed Grouse, Prairie Chickens initially prospered and rapidly followed agriculture northward, colonizing North Dakota in the 1870's (Johnson, 1964), and reaching Manitoba, Saskatchewan and Alberta by 1900 (Rowan, 1926). They also extended westward across Nebraska and Kansas to northern Colorado, which represents the original range of the Lesser Prairie Chicken. Almost as quickly as they flourished, Prairie Chickens began to suffer from the effects of too intensive agriculture. After peaking near the turn of the century, they quickly declined and disappeared from northwestern Ohio before 1930 (Leopold, 1931) as well as being exterminated from Kentucky, Arkansas and Texas. The last known active booming ground in Iowa was seen in 1954 (Stempel and Rodgers, 1961), and only a tiny handful of birds still remain in Indiana (Hamerstrom and Hamerstrom, 1961).

An attempt has been made to plot the present distributions of Prairie Chickens and Sharp-tailed Grouse (Fig. 3), based on a review of the recent literature. Particular attention has been paid to those areas of probable current sympatry, and less concern has been given to those parts of the west where Prairie Chickens have never occurred. Some recent state distribution maps or range descriptions for one or both species have been published and provide more details than could be shown here. Thus, relatively detailed state maps or statements of status are available for Sharp-tailed Grouse in the western states of Washington (Yocom, 1952), Oregon (Masson and Mace, 1962), Nevada (Gullion and Christensen, 1957), Montana (Anon., 1959), Colorado (Ryder, 1960; Bailey and Niedrach, 1965), and Utah (Hart et al., 1950). Similarly, recent range maps have been published for the Attwater's Prairie Chicken (Lehmann and Mauermann, 1963), and for the Lesser Prairie Chicken in Colorado (Hoffman, 1963), Kansas (Baker, 1953), Oklahoma (Copelin, 1963), and Texas (Jackson and DeArment, 1963).

The distribution of the Greater Prairie Chicken (Fig. 3) has obviously shrunk alarmingly, even during the last decade. Thus, it now appears to be almost completely gone from western Canada (Hamerstrom and Hamerstrom, 1961), and has retreated from the western limits of its acquired range in the Dakotas and Nebraska. A series of detailed maps showing historical changes in Prairie Chicken and Sharp-tailed Grouse ranges has been published for Michigan (Ammann, 1957). Historical changes in Prairie Chicken ranges and abundance have also been documented for Ontario (Lumsden, 1966), Kansas (Baker, 1953), Missouri (Bennett and Nagel, 1937; Schwartz, 1945), Iowa (Stempel and Rodgers, 1961), Illinois (Yeatter, 1943, 1957, 1963),

FIG. 3. Present ranges of Sharp-tailed Grouse (shaded) and Prairie Chickens (stippled) in southern North America, based on published and unpublished information through 1966.

Wisconsin (Schorger, 1944; Grange, 1948; Hamerstrom et al., 1957), North Dakota (Johnson, 1964), and to some degree for Nebraska (Viehmeyer, 1938, 1941; Beck, 1957; Kobriger, 1965). The current status of the two species of prairie grouse in Minnesota has been shown by Farmes et al. (1960), who indicate that the Prairie Chicken is largely restricted to the eastern edge of the Red River valley between Polk and Wilkin counties, where there is little contact with Sharp-tailed Grouse. Mr. James L. Ruos (letter of 28 April 1966) indicated that, although no hybrid specimens are in the Minnesota Game and Fish Collections, about one bird out of every 600 Sharp-tailed Grouse shot is of hybrid appearance. Grouse are not hunted within the major part of Minnesota's Prairie Chicken range. Prairie Chickens have been protected in North Dakota since 1945 (Johnson, 1964), and now occupy a discontinuous range in a few eastern counties such as Stutsman, Ransom, and Grand Forks, where Sharptail populations are only fair to poor (G. D. Kobriger, letter of 22 March 1966). Both species occur in numbers large enough to be regularly harvested in South Dakota, but even in that state the Prairie Chicken occupies a relatively restricted and probably diminishing range, and it is now primarily limited to areas of tall grasses in Gregory, Lyman, Tripp, and Jones counties (Henderson, 1964). Here, average rainfall is somewhat higher than in other counties west of the Missouri River, but agricultural land-use has not been as intensive as in those counties east of the river (Janson, 1953). Thus, in Nebraska alone both species are still sufficiently widespread and common to be major game species.

The geographic distribution of Prairie Chickens and Sharp-tailed Grouse in Nebraska appears to be a fairly stable one at present. Although Prairie Chickens at one time may have occurred nearly throughout the state (Bruner et al., 1904), it is probable that they never became as common as Sharp-tailed Grouse in the extensive sandhills region of central and western Nebraska. Rather, they evidently penetrated into the sandhills wherever grain crops were planted and supplemented the native grasses, and in particular they probably followed the river systems northwestward into the interior of the sandhills. A range map published by Mohler in 1944 suggests a close relationship between the range of Prairie Chickens and the geographic distribution of the sandhills. With minor changes, including a retraction of the western limits of the range and an inclusion of a few small Prairie Chicken colonies in the southeastern corner of the state that represent the northern limits of the large Flint Hills population of Kansas, his map would probably adequately serve to describe the species' present Nebraska range. But the Prairie Chicken is not so much a bird of the sandhills as it is of their perimeter and, in particular, of their southern and eastern edges, where native grasses and grain crops interdigitate

along a broad front. Thus, counties such as Holt, Rock, Garfield, and Wheeler, which border on the sandhills and have an average of 20 or more inches of rainfall (U. S. Dept. of Agriculture, 1941) are the ones having the greatest concentrations of Prairie Chickens. On the other hand, Sharp-tailed Grouse seem to survive best on Nebraska's undisturbed grassland, and probably not only originally occurred (Bruner et al., 1904) but also still exist primarily in those drier western counties that are largely or entirely still covered with native grasses.

INTERSPECIFIC HYBRIDIZATION AND MIXED DISPLAY GROUNDS

Presumably because of the minor presettlement geographic overlap and the apparent ecological segregation where such overlap occurred, probably little if any hybridization originally occurred between Prairie Chickens and Sharp-tailed Grouse. The first reported hybrid was described in 1877 by W. Brewster, based on a specimen obtained in Iowa. A few years later, a second hybrid was described (Gurney, 1884), but its place of origin was unknown. Supporting the view that prior hybridization must have been rare is the fact that this later specimen was the first that Elliott Coues had ever encountered, in spite of his extensive travels in the upper Great Plains. Bent (1932) reported examining four hybrids obtained in the Boston markets between 1873 and 1893. Several hybrids have been reported for North Dakota (Gross, 1930), including one killed in 1923 (Bent, 1932). An early hybrid from Colorado was described by F. C. Lincoln in 1918, and more recently another was observed on a Prairie Chicken display ground by Evans (1966). Rowan (1926) reported two hybrid specimens from Alberta, and indicated that hybrids were more frequent in Manitoba. Several hybrids from Saskatchewan are also known (Rowan, 1926; Ammann, 1957).

A number of hybrids have been reported from Wisconsin (Gross, 1930; Ammann, 1957), and about 50 were identified during 13 years of field work in Michigan by Department of Conservation personnel (Ammann, 1957). Mr. Fred A. Priewert, of the South Dakota Department of Game, Fish, and Parks, has provided data (letter of 1 April 1966) indicating that ten identified hybrids were noted among 1,534 grouse banded in Gregory and Lyman counties between 1962 and 1966. Hybrids have also been observed on display grounds in South Dakota; at least 13 were counted on 10 Sharptail grounds (with 133 male Sharptails) and four hybrids were observed on four Prairie Chicken grounds with 36 of the latter (F. R. Henderson, letter of 26 April 1966). Perhaps the highest known incidence of current hybridization is to be found on Manitoulin Island in Lake Huron, where the previously isolated Sharptail race *P. p. phasianellus* from Ontario has recently come into contact with the

Prairie Chicken (H. G. Lumsden, letter of 27 February 1966), resulting in extensive hybridization. On this island possibly 80 per cent of the birds on Prairie Chicken display grounds are not typical Prairie Chickens (Ammann, 1957), and altogether between five and 25 per cent of the population may be hybrids (Mayr, 1963, p. 117).

There are no published records of the early occurrence of hybrids in Nebraska, but the University of Nebraska museum has an obvious hybrid obtained in Cherry County in 1926. An estimated three or four obvious hybrids are noted out of 600 to 1,000 grouse that are observed yearly by Nebraska Game, Forestation and Parks Commission personnel at hunter check stations, but others might easily go unnoticed. In 1966 two probable hybrids were observed among a total of 507 male grouse on display grounds closely examined for possible hybrids. Game Commission records of grouse trapped between 1959 and 1965 indicate that 936 Sharp-tailed Grouse, 310 Prairie Chickens and 15 hybrids were obtained. These figures suggest a minimum hybridization rate of between 0.3 per cent and 1.2 per cent in recent years, or considerably below that now occurring on Manitoulin Island. The fact that contact between the species there may not have been sufficiently prolonged to have allowed a reinforcement of isolating mechanisms (H. G. Lumsden, in litt.), and that assortative mating opportunities may be more limited on that island, might largely account for the marked differences in hybridization rates between the two areas.

Even in the absence of actual hybridization, interaction may occur between the two species in the form of attraction of males to the other's display grounds. Thus, the proportions of single-species and mixed display grounds in areas where both forms occur might provide an indication of the relative degree of reproductive isolation between the species. Such mixed grounds have been previously reported from various areas. Lumsden (1965) mentions the occurrence of mixed grounds on Manitoulin Island, and Ammann (1957) noted that a Prairie Chicken ground in Michigan was later taken over by Sharptails. In Wisconsin, Hamerstrom (1939) reported three mixed grounds among a total of 33 display grounds, and Grange (1944) found numerous mixed display grounds. During 1941 and 1942 Grange observed a total of 19 "hooting" or "dancing" grounds used by Sharp-tailed Grouse only, 58 Prairie Chicken "booming" grounds, and five mixed display grounds that were used by both species each of the two years. Of 13 additional mixed grounds that were used in 1941, ten changed to pure Sharp-tailed Grouse grounds in 1942, and three changed to pure Prairie Chicken grounds. Moreover, three grounds changed from single-species grounds to mixed grounds between 1941 and 1942, and one ground occupied by Prairie Chickens in 1941 was used

only by Sharp-tailed Grouse in 1942. Four mixed grounds studied in 1942 had an average total of eight males present, but ranged from two to 11 males. Two of the four had only a single male of one or both species, and the other two had a minimum of three males of each species. Altogether, Grange observed 30 grounds (almost 16 per cent of the total) that were used jointly one or both years, compared with 68 Sharp-tailed Grouse grounds and 94 Prairie Chicken grounds that were used one or both years, if double allowance is made for grounds that changed in status and thus might be counted twice. Considering both years, Grange provides estimated total population figures that suggest an average proportion of about 37 per cent Sharptails to 63 per cent Prairie Chickens.

The existence of mixed display grounds in Nebraska was first documented by Mathisen and Mathisen (1959), who reported that during three years (1955 to 1957) 13 such grounds were observed by Game Commission personnel. Interestingly, the majority of these mixed grounds occurred in those counties where both species are relatively abundant, suggesting that interaction and perhaps hybridization are more likely in such areas than in regions where one species is relatively rare. This same phenomenon also appears to be true of hybridization between Mallards (*Anas platyrhynchos*) and Black Ducks (*Anas rubripes*) (Johnsgard, 1967).

Data on the male grouse constitution of a total of 72 mixed display grounds from Nebraska and South Dakota were available to us, including the 13 grounds listed by Mathisen and Mathisen (1959), records of 58 additional grounds (some of which represent the same grounds counted in different years between 1958 and 1966) in the files of the Nebraska Game Commission, plus records of several mixed grounds from South Dakota provided by F. Robert Henderson and Warren Jackson. These 72 grounds had an average total of 9.8 males present (range two to 22), but had an average of only 2.0 males of the rarer species (range one to six), indicating that many mixed grounds (33 out of 72) contained only a single male of the rarer species. There were an average of 5.3 Prairie Chicken males on these mixed grounds, and in 24 cases this species was the rarer form. On the other hand, there were an average of 4.3 Sharp-tailed Grouse males on the grounds, and in 46 cases this species was the rarer form. In the two remaining instances the species were represented in equal numbers. This difference would suggest that Sharp-tailed Grouse may be more prone to enter Prairie Chicken grounds than is the reverse situation. A chi-square test on the greater than expected frequency of Sharp-tailed Grouse over Prairie Chickens occurring as the rarer form indicates that such a differential response is highly probable ($P < 0.01$).

Hybrid males have been observed on a number of mixed and pure display

grounds in Nebraska and South Dakota. Thirteen of 26 such observations were made on Sharp-tail grounds, six involved Prairie Chicken grounds, and on seven occasions hybrids were observed on mixed display grounds.

Some data on the geographic distribution of mixed display grounds in Nebraska are now available, as a result of intensive Game Commnssion surveys in three areas. These include the National Forest near Halsey in Thomas and Blaine counties, an area near Swan Lake in Holt County, and an area in southeastern Loup County. The relative numbers of pure and mixed display grounds, and total numbers of grouse counted on them, are shown in Table 1 which is largely based on unpublished Game Commission data provided by Mr. Lawrence Blus. In addition, figures for ten Game Commission spring survey areas in the eastern sandhills are included for the years 1963 to 1966.

TABLE 1

OCCURRENCE OF MIXED DISPLAY GROUNDS IN NEBRASKA

Area	Average No. of display grounds			Total average No. of males	
	Dancing	Booming	Mixed (%)	Sharp-tails (%)	Prairie Chickens (%)
National Forest (1962–1965)	35	0.75	0.5 (1.8%)	223 (99.12%)	1.9 (0.78%)
Loup County (1959–1962)	11	6	3.5 (17%)	159 (67.6%)	86 (32.3%)
Swan Lake (1959–1962)	3.5	17	1 (4.6%)	27.5 (16.8%)	141 (83.2%)
Various counties (1963–1966)	16	51	7 (9.4%)	158 (24%)	498 (76%)

In this table a direct relationship between the frequency of mixed grounds and the relative abundance of the less common species is clearly apparent. In theory, mixed display ground frequency should be related both to this ratio and to the average total number of males present on a ground. Thus, if no preferential attraction of males to display grounds of their own species exists, it would be mathematically expected that, where both species are equally common, a display ground containing nine males should be composed entirely of one species or the other only once in 256 instances (0.39%). Display grounds containing smaller numbers of males would have a higher expected proportion of unmixed assemblages, as would grounds in areas where one form is distinctly rarer than the other (Fig. 4).

In an attempt to determine whether the available data fit the hypothesis that the occurrence of mixed display grounds follows such an expanded binomial distribution pattern, the relationship between their frequency and the

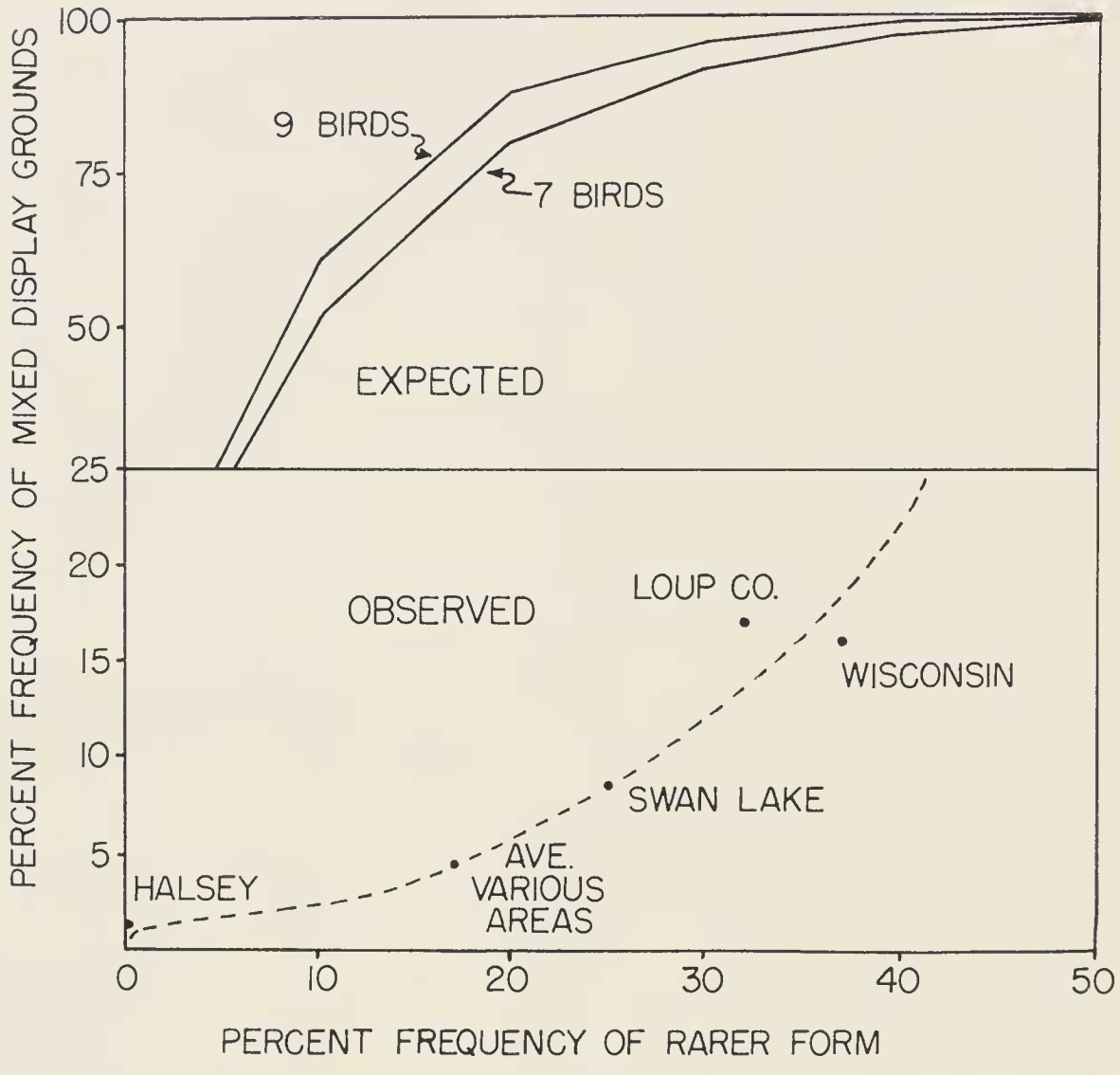

Fig. 4. Comparison of observed incidence of mixed display grounds (below) and calculated incidence expected on the basis of random aggregation and relative abundance of the two species of grouse (above).

frequency of the rarer species has been plotted for the Nebraska areas listed in Table 1 as well as for Wisconsin, based on the figures provided by Grange (1944). Average display ground sizes reported by Grange varied from six to eight birds, and in total averaged about seven. The overall average display ground size for the grounds listed in Table 1 is 9.1 males, and this range of values is about the same as those reported for both species in other states (Ammann, 1957; Yeatter, 1943). A line fitted visually to the points provided by the available data (Fig. 4) supports the contention that mixed display grounds are most prevalent in areas where both species occur commonly, although their apparent frequency is far lower than would be expected if random aggregation of males actually occurs. This difference suggests that

males of either species are several times more likely to be attracted to display grounds occupied by others of their kind than to those of the other species.

Of equal or greater interest than the aggregation patterns of displaying males is the probable differential attraction of females of both species to the various types of display grounds, and the relative success of males in fertilizing females of their own species on mixed grounds. Mr. Lawrence Blus informed us that on 14 May 1962 he observed a female Prairie Chicken enter a display ground containing five Sharp-tailed Grouse and a single male Prairie Chicken. The female walked past at least two of the Sharp-tailed Grouse, one of which displayed directly toward her, and stopped in front of the Prairie Chicken, where copulation occurred almost immediately. It is hoped that additional observations on this aspect of the problem will be obtained, and that the reproductive success of hybrids might also be determined.

SUMMARY

A comparison of probable presettlement and present distributions of Sharp-tailed Grouse and Greater Prairie Chickens suggests that their original, probably narrow, zone of sympatric distribution has greatly enlarged as a direct result of land-use changes associated with agriculture. Ecological differences exist in areas of current sympatry that reduce actual interspecific contact, but hybrids have been reported from every state and province where sympatry has occurred. In Nebraska the current minimum rate of hybridization is estimated at between 0.3 and 1.2 per cent of the combined grouse population. A considerable number of display grounds used by both species in the state, and the incidence of such mixed display grounds is directly related to the relative frequency of the rarer species in local areas. The highest known incidence (17 per cent) of mixed grounds in Nebraska occurs where the rarer species comprises almost a third of the total population; this situation compares closely with estimates based on data from Wisconsin. Although a strong tendency exists for males of both species to form single-species rather than mixed aggregations, Sharp-tailed Grouse have been observed to be the intruder species on Prairie Chicken grounds significantly more frequently than the reverse situation. Records of 72 mixed grounds in Nebraska and South Dakota indicate they were of about the same average size as single-species grounds (9.8 vs. 9.1 males), and an average of only 2.0 males of the rarer species were present.

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